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## THE CONTINUOUS ORIGIN OF CERTAIN UNIT CHARACTERS AS OBSERVED BY A PALEONTOLOGIST<sup>1</sup>

DR. HENRY FAIRFIELD OSBORN

RESEARCH PROFESSOR OF ZOOLOGY, COLUMBIA UNIVERSITY, CURATOR EMERITUS  
OF VERTEBRATE PALEONTOLOGY IN THE AMERICAN MUSEUM OF  
NATURAL HISTORY, VERTEBRATE PALEONTOLOGIST  
UNITED STATES GEOLOGICAL SURVEY

### II. EVIDENCES FOR CONTINUITY

Abandoning the historical background, we come to our own subject, *the origin and establishment in continuity of characters which when established exhibit many of the distinctive features of unit characters, namely, segregation, stability, pure heredity, and possibly, although this has not yet been demonstrated, dominance and recession in successive generations.*

In fifteen previous papers of the writer beginning in 1889<sup>25</sup> the observation is repeatedly made that all absolutely new characters which we have traced to their very beginnings in fossil mammals arise gradually and continuously. One by one these characters, which are independently changing in many parts of the organism, at the same time accumulate until they build up a degree of change which paleontologists designate as a "mutation"

<sup>25</sup> Osborn, H. F., "The Paleontological Evidence for the Transmission of Acquired Characters," AMER. NATURALIST, Vol. XXIII, No. 271, July, 1899, pp. 561-566.

in the sense of Waagen, who proposed this inter-specific term in 1869. Finally they reach a sufficiently important phase to designate the stage as a species.<sup>26</sup>

These new characters were first (1891) termed "definite variations"; subsequently (1907)<sup>27</sup> the term "rectigradations" was applied to them. Rectigradation is merely a designation for the earliest discernible stages of certain absolutely new characters. It involves no opinion nor hypothesis as to genesis; it is a simple matter of observation. Referring to the figure (p. 274) of the upper grinding teeth of the horse, the majority of the fourteen characters have been observed to arise as rectigradations.

Quite different is the allometron. This is a new designation for the continuous change of proportion in an existing character which may be expressed in differences of measurement. Since 1902 and especially during the past year the behavior of allometrons has been very carefully investigated by myself and by my colleague, Dr. W. K. Gregory.

RECTIGRADATION = a qualitative change, the genesis  
of a new character.

ALLOMETRON = a quantitative change, the genesis  
of new proportions in an existing character.

The distinction between a rectigradation and an allometron is readily grasped: when the shadowy rudiment of a cusp or of a horn first appears it is a rectigradation; when it takes on a rounded, oval or flattened form this

<sup>26</sup> This sentence may be contrasted with that of Punnett (*op. cit.*, p. 15): "Speaking generally, species do not grade gradually from one to the other, but the differences between them are sharp and specific. Whence comes this prevalence of discontinuity if the process by which they have arisen is one of accumulation of minute and almost imperceptible differences? Why are not intermediates of all sorts more abundantly produced in nature than is actually known to be the case?"

<sup>27</sup> Osborn, H. F., "Evolution of Mammalian Molar Teeth to and from the Triangular Type," 8vo, Macmillan Company, September, 1907.

change is an allometron. In mammals rectigradations are comparatively few; allometrons comprise the vast number of changes in the hard parts. In the origin of cusp and horn rudiments rectigradations are parallel (see Fig. 3), in the changing proportions of a skull allometrons are divergent (Figs. 1, 3).

Granting, without at present considering the evidence,<sup>28</sup> that these rectigradations and allometrons arise continuously through entirely unknown laws, that they are blastic or germinal characters, the question arises, do they become separable as unit or alternating characters in heredity.

In general, paleontology furnishes quite as strong proof as Mendelism or experimental zoology *as to the individuality, separableness, and integrity of single characters in evolution*. But, whether both rectigradations and allometrons are separable in heredity can only be demonstrated through experiments on cross breeding or hybridizing.

The special object of this Harvey lecture is to show that certain at least of the rectigradations and allometrons observed in mammals are separable in heredity, that they split up into larger and smaller groups or units, some into partially blending units, others into absolutely distinct or non-blending unit; finally that at least in the first cross they exhibit dominance.

The very important remaining question whether, like the quality of "tallness" or "shortness" in Mendel's classic experiments on the pea, these allometrons continue to split into dominants and recessives in later crosses, has not been investigated but is probably capable of investigation in mammals which do not become sterile in the first hybrid generation.

Five examples of the continuous evolution of rectigradations and allometrons may be cited, namely:

<sup>28</sup> This evidence is for the first time fully presented in the writer's monograph on the "Titanotheres," in preparation for the U. S. Geological Survey.

1. Skull and horns of titanotheres (Figs. 1, 3, 4).
2. The horns of cattle (Fig. 2).
3. The cranium of man (Fig. 1).
4. The skull of horses (Figs. 4, 5, 6, 7).
5. Teeth (Fig. 8).

One of the most salient examples of the genesis of unit characters through continuity is that of the evolution of horns, *i. e.*, of the osseous prominences on the skull. Horns are now known definitely to be "unit characters," first through their sudden and complete disappearance in the niata and polled breeds of cattle; second, because they conform to the laws of sex-limited inheritance. The question is, do horns originate continuously or discontinuously?

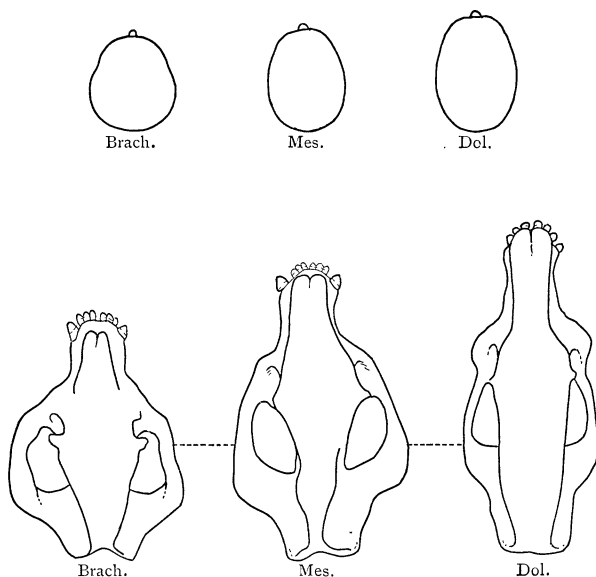


FIG. 1. CONTINUOUS ORIGIN OF ALLOMETRIC "UNIT CHARACTERS" IN THE CRANIUM (A) AND SKULL (B) OF MAN AND TITANOTHERES.

A, Man	Brachycephaly	Mesaticephaly	Dolichocephaly
B, Titanotheres	Brachycephaly ( <i>Paleosyops</i> )	Mesaticephaly ( <i>Manteoceras</i> )	Dolichocephaly ( <i>Dolichorhinus</i> )

### 1. Horns of Titanotheres

The titanotheres are an extinct family of quadrupeds distantly related to the horses, tapirs and rhinoceroses,

to the evolution of which the author has devoted twelve years of investigation, assisted by Dr. W. K. Gregory. As set forth in an earlier contribution<sup>29</sup> the genesis of horns as rectigradations has been observed in four or five distinct phyla of titanotheres. These phyla descend independently from a single ancestor of remote geologic age. Both in respect to new cusps on the teeth and new horn rudiments on the skull there is observed what in our ignorance may be called an ancestral predisposition to the genesis of similar rectigradations. This predisposition betrays the existence of *law* in the origin of certain new characters; it recalls a sagacious remark of Darwin:

. . . The principle formerly alluded to under the term of *analogical variation* has probably in these cases often come into play; that is, the members of the same class, although only distantly allied, have inherited so much in common in their constitution, that they are apt to vary under similar exciting causes in a similar manner; and this would obviously aid in the acquirement through natural selection of parts or organs, strikingly like each other, independently of their direct inheritance from a common progenitor.<sup>30</sup>

Briefly, the origin of the titanothere horns is as follows: (*a*) from excessively rudimentary beginnings, *i. e.*, rectigradations, which can hardly be detected on the surface of the skull; (*b*) there is some predetermined law or similarity of potential which governs their first existence, because (*c*) the rudiments arise independently on the same part of the skull in different phyla at different periods of geologic time; (*d*) the horn rudiments evolve continuously, and they gradually change in form (*i. e.*, allometrons); (*e*) they finally become the dominant characters of the skull, showing marked variations of form in the two sexes; (*f*) they first arise in late or adult stages of growth, but are pushed forward gradually into

<sup>29</sup> "The Four Inseparable Factors of Evolution. Theory of their Distinct and Combined Action in the Transformation of the Titanotheres, an Extinct Family of Hoofed Animals in the Order Perissodactyla," *Science*, N. S., Vol. XXVII, No. 682, January 24, 1908, pp. 148-150.

<sup>30</sup> "Origin of Species," Vol. II, p. 221.

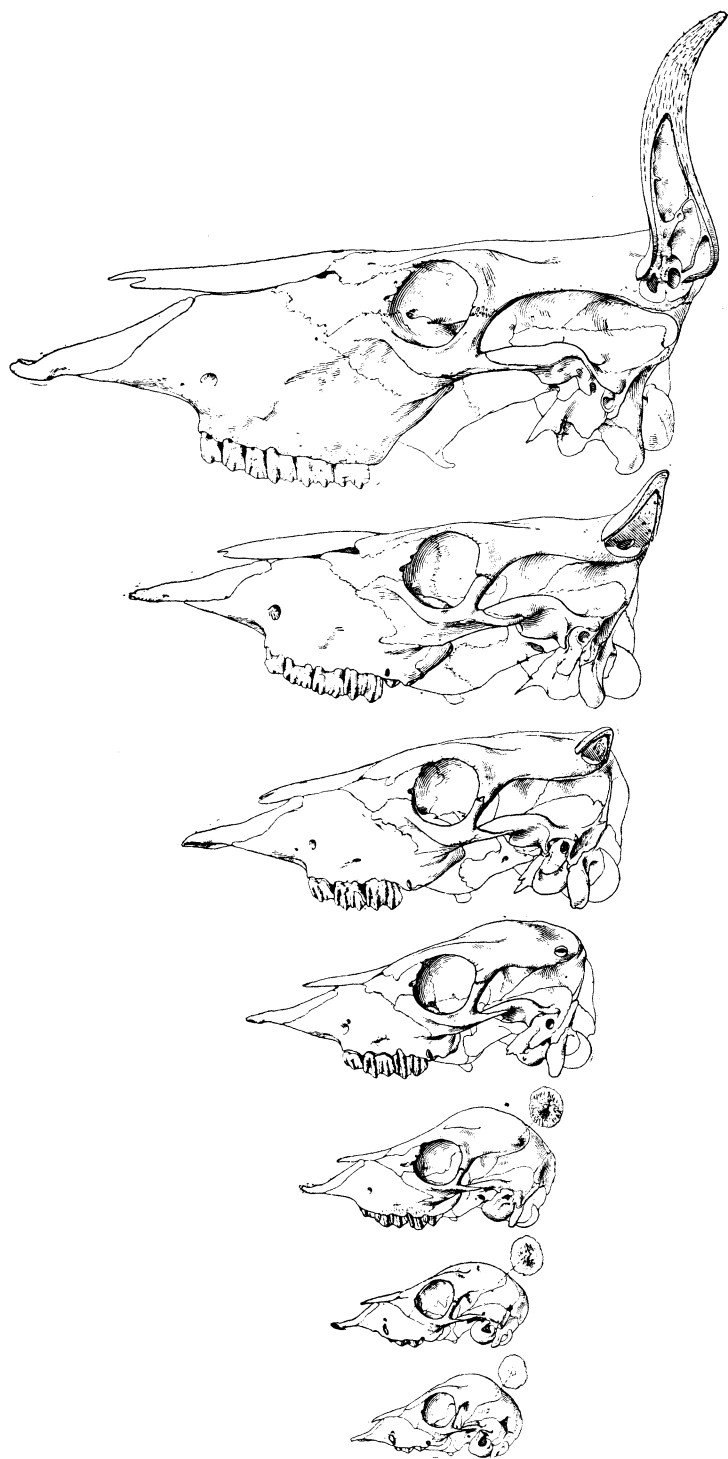


FIG. 2. CONTINUITY IN THE ONTOGENESIS OF THE HORN AND HORN SHEATH IN CATTLE IN SEVEN STAGES, 1-7. After preparations by Mr. S. H. Chubb in the collections of the American Museum of Natural History.

1. Adult, 9 years, completed osseous horn and horny sheath. 2. Yearling, 18 months, continuous shifting of osseous horn to occiput. 3. Calf, 2 months, continuous shifting of osseous horn to occiput. 4. Calf, 9 months, bony swelling, and epidermal swelling pointed. 5. Foetal stage, 2 weeks, pointed hair tuft. 6. Foetal stage, 46-74 months, epidermal swelling, covered with pointed hair tufts. 7. Foetal stage, 25 months, epidermal swelling, covered with 40 scattered hairs.

earlier and earlier ontogenic stages until they appear to arise prenatally.

In the titanotheres (Fig. 3) the bony swelling is seen at the junction of the nasals and frontals (black shading), in dolichocephalic skulls it appears chiefly on the nasals, in brachycephalic skulls chiefly on the frontals. Its original low, rounded shape is like that seen in the ontogeny of the horns in cattle.

## 2. *Horns of Cattle*

The phylogenesis of the horns in titanotheres (Fig. 3) is exactly similar to the ontogenesis of the horns in Bovidae (Fig. 2), in which the dermal rudiments first appear soon after the complete formation of the bones of the skull in the unborn young, and the osseous rudiments appear as rounded protuberances in the 8th month.

In the ontogenesis of horns in cattle three distinct elements are involved: (*a*) a psychic predisposition to use the horn, (*b*) a dermal thickening over the bony horn swelling which in ontogeny precedes the swelling, (*c*) appearance of the bony swelling itself.

The ontogenesis is observed to be accompanied by a marked allometric change in the skull which shifts the horn backward from the side of the cranium to the side of the occiput by the obliteration of the parietal bones.

## 3. *Cranium of Man.*

A third instance of continuous development is that of the form of the cranium in man (Fig. 1), an allometric evolution, or change of proportion, which is of especial significance because, according to the unanimous testimony of anthropologists,<sup>31</sup> head form is the result of very gradual change either in the elongate (dolichocephalic) or broadened (brachycephalic) direction.

<sup>31</sup> Ripley, Wm. Z., "The Races of Europe, a Sociological Study," 8vo, D. Appleton & Co., 1899, 624 pp.

The matter is directly pertinent to the present discussion because "long heads" and "broad heads" are continuously crossing and we know what the direct and ultimate effects of such crosses are. The evidence has important bearing also on the influence of selection, environment, and inheritance or the effects of use and disuse.

Determination of the proportions of the cranium or the cephalic index is one of the standard tests of race; it is an expression of the greatest breadth of the head above the ears and the percentage of its greatest length from the forehead (glabella) to back, the latter measurement being taken as 100. Three types adopted by anthropologists are:

	Extreme Range
Brachycephalic, 80.1 and above .....	100-80
Mesocephalic, 75.1-80 .....	80-75
Dolichocephalic, 75 and below .....	75-62

Among the present races of Europe the widest limits of variation between brachycephaly and dolichocephaly are in the averages between 73 and 87; individual extremes of 62 and 100 have, however, been observed. These extremes in European head form do not coincide either with geographic or political boundaries, but are attributed to the entrance into Europe of brachycephalic and dolichocephalic types which evolved in Asia. Similarly among the aborigines in America the indices range from a low dolichocephaly as among the Delaware, Pima Indians, etc., to a decided brachycephaly as among the Athabascan tribes in Panama, Peru, and other localities. A significant fact in Europe is that dolichocephaly and brachycephaly are extremely stable characteristics in heredity. The significant fact in America is that through a very long period of time the various races of Indians, who are believed to have had originally a similar origin, have acquired under conditions of geographic isolation considerable diversity in the proportions of the head. Similarly A. Keith<sup>32</sup> from the present distribution of the

<sup>32</sup> Keith, A., *Journ. Royal Anthropological Institute*, 1911. See *Nature*, Vol. 88, No. 2195, November 23, 1911, p. 119.

Negro tribes in equatorial Africa has reached the following conclusions:

There has been free intermigration; in the course of their evolution, the tendency of one tribe has been towards the accentuation of one set of characters, of another towards another set. Thus the Dinka acquire high stature and narrow heads; the typical Nigerians low stature and narrow heads; the Basoko wide, short heads and low stature; the Buruns wide heads and high stature. Interbreeding may have played its part; but if it had played a great part we should have found greater physical uniformity than there is. The influence of Arab blood on these tribes has probably been exaggerated.

It appears that environment has not any direct influence on head form, but that geographical isolation affords the several varieties of man as well as other mammals a chance to develop their peculiar head characters. Elliot Smith states (letter, August 12, 1911):

In my opinion the conditions of dolichocephaly and brachycephaly must have developed very slowly through exceedingly long periods of time and in widely separated areas amidst widely different environments. Brachycephaly is especially distinctive of the Central Asian high plateau populations, dolichocephaly of the littoral and plain-dwelling peoples; but these "unit characters" are now so fixed that environment is powerless to modify them in a thousand years or so. . . . I do not believe for a moment in Boas [that is, in Boas's observations (1911) on the rapid influence of environment in modifying head form].

Elliot Smith takes very strong ground as to the lack of evidence that environment directly produces any modification of head form; he implies that such modification, if natural, would only show itself after thousands of years of residence; environment no doubt has indirect influence. Hrdlička, on the other hand, has obtained definite results in the influence of environment on the vault and face form of the Eskimo;<sup>33</sup> it remains to be shown how far these changes are ontogenic. The recent conclusions of Boas (1911)<sup>34</sup> that dolichocephaly and brachy-

<sup>33</sup> Hrdlička, Ales, "Contribution to the Anthropology of Central and Smith Sound Eskimo," *Anthr. Paper Am. M. N. H.*, V, Pt. II, 1910, p. 214.

<sup>34</sup> Boas, Franz, "The Mind of Primitive Man," 8vo, Macmillan Company, New York, 1911, 924 pp.

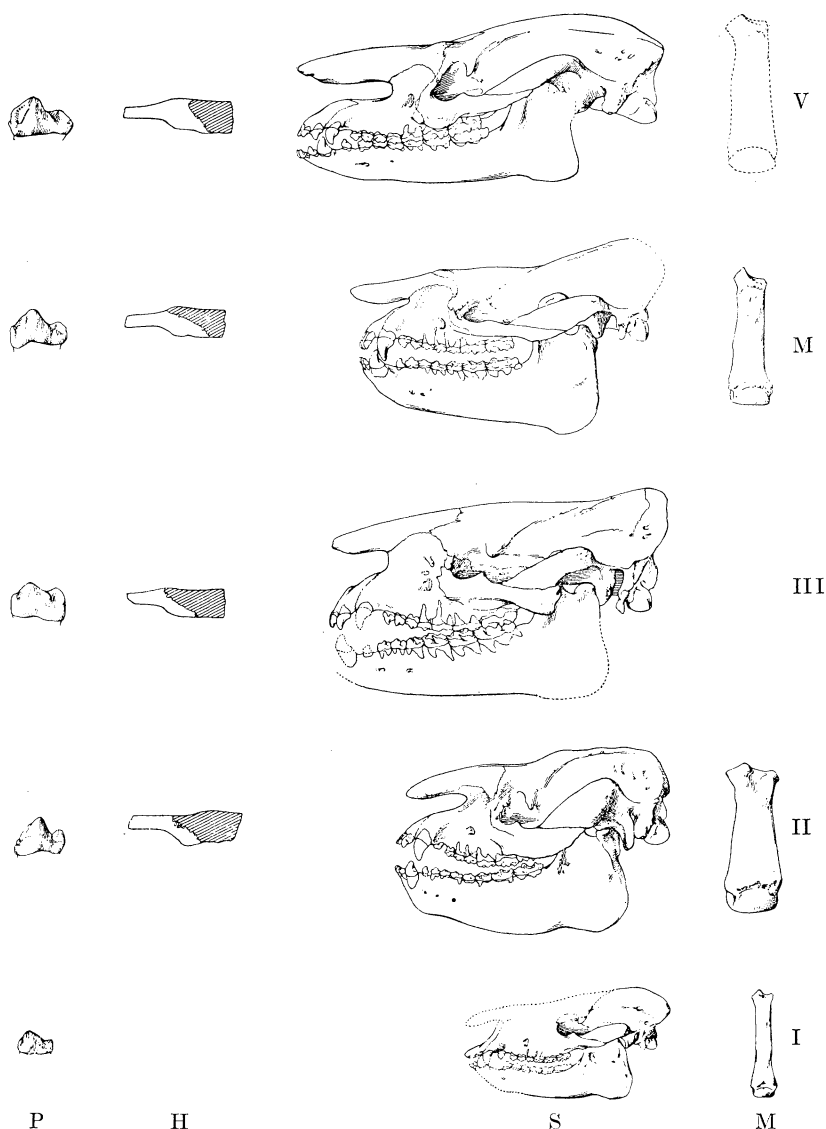


FIG. 3. RECTIGRADATIONS AND ALLOMETRONS IN TITANOTHERES. Continuity in the phygenesis of osseous horns in titanotheres. *P* = 2d lower premolar; *H* = section of nasals and frontals (shaded) showing osseous horn; *S* = skulls; *M* = median metacarpal bones.

V. *Dolichorhinus*, a long-headed (dolichocephalic) titanotheres.

IV. *Mantoceras*, a medium-headed (mesaticephalic) titanotheres.

III. *Telmatherium*, a medium-headed (mesaticephalic) titanotheres.

II. *Palaeosyops*, a broad-headed (brachycephalic) titanotheres.

I. *Eotitanops*, an ancestral (mesaticephalic) titanotheres.

II-V belong to four independent phyla which diverge in their allometric evolution of head (*S*) and foot proportion (*M*) but give rise to independent similar rectigradations in the origin of cusps on the premolar teeth (*P*) and of osseous horn rudiments (*H*) on the skull.

cephaly are congenitally altered by environment in the first generation are modified by his statement that this action in bringing diverse head forms together would not go so far as to establish a uniform general type.

No anthropologist has offered any satisfactory explanation as to the adaptive significance of dolichocephaly or brachycephaly. It is well known that these differences of head form are not associated with intellectual ability or mental aptitude. Boas writes (April 8, 1911):

So far the matter is very perplexing to me. I feel, however, very strongly with you that changes in type are very liable to be progressive in definite directions. . . . To my mind it seems no more difficult to assume that this predetermined direction should continue from generation to generation than to make the much more difficult assumption that notwithstanding all internal changes the egg-cell of one generation should be absolutely identical with that of the preceding generation.

Apart from the disputed question of the direct influence of environment and of human selection there is absolute unanimity of evidence and of opinion on the one point essential to the present discussion, namely, *as to the continuity of allometric variation which establishes different extremes of head form under conditions of geographic isolation.*

Granted that these extremes evolve continuously, do they become discontinuous in heredity?

One of the general results of crossing long-headed and narrow-faced types with broad-headed and broad-faced types is what is known as disharmonic heredity, namely, that condition in which the face and cranium do not hold together, but broad faces may couple with long skulls, or *vice versa* (Boas, 1903).<sup>35</sup> Boas concludes that there can be no question that the mixture of a long-headed and of a short-headed race may lead to disharmonism, one race contributing head form, the other facial expression.

As to stability or segregation in heredity the latest

<sup>35</sup> Boas, Franz, "Heredity in Head Form," *Amer. Anthropologist*, Vol. 5, No. 3, July-September, 1903, pp. 530-538.

opinions of Boas, Elliot Smith and Hrdlicka have been sought. Boas is one of the most positive as to the hereditary stability of head form. He observes (1911, pp. 7-9):

Among European peoples head proportions are considered among the most stable and permanent of all characteristics. In intermarriage of "dolichocephalic" and "brachycephalic" individuals the children do not form a blend between their parents but inherit either the dolichocephalic or brachycephalic head form. Head form thus constitutes a case of almost typical alternating heredity (p. 55). No evidence has been obtained, however, to show that either brachycephaly or dolichocephaly is dominant. Children exhibit one head form or the other, and the cephalic index or ratio of breadth to length undergoes only slight alteration during growth, or ontogeny.

Elliot Smith (letter of August 12, 1911) is "firmly convinced that the form of cranium, orbits, nose, jaws, limb bones, etc., in the 'Armenoid' and 'Proto-Egyptian' series are very stable or even fixed 'unit characters' which do not really blend, but that certain elements of mosaic assemblage of characters may be grafted on to others belonging to the other race."

*Opinions as to Blending.*—It will be noted that Boas (1895) admits a certain blending of head form in crosses. Hrdlička (letter, November 1, 1911) speaks even more guardedly as to the hereditary stability of head form. He says:

As to the head form constituting a "unit character" which does not blend in intermixture, I am not able to give a conclusive opinion, but my experience and other considerations lead me to be very skeptical that such is the case to any great extent. The subject is a very complex one and requires considerable direct investigation in different localities and with different peoples before the exact truth can be known. . . . As to the statement that long or broad head form is a stable or unit character not blending in intermixture, I think that only the first part of the proposition may be held as fairly settled. But even then I should change the word "stable" to "persistent," and qualify the phrase by adding "under no greatly differing and lasting environmental conditions."

That prolonged interbreeding or intermixture tends to break down the stability of hereditary head form is

indicated by Boas, Elliot Smith, and Ripley, as well as by Hrdlička, as quoted above. Thus Ripley (1899), p. 55) observes:

The plotting of cephalic indices on a map of Europe shows that there is a uniform gradation of head form from several specific centers of distribution outward.

In Italy over 300,000 individuals taken from every little hamlet have been measured. In the extreme south we find the dolichocephalic head form of the typical Mediterranean race; the type changes gradually as we go north until in Piedmont we find an extreme of brachy-

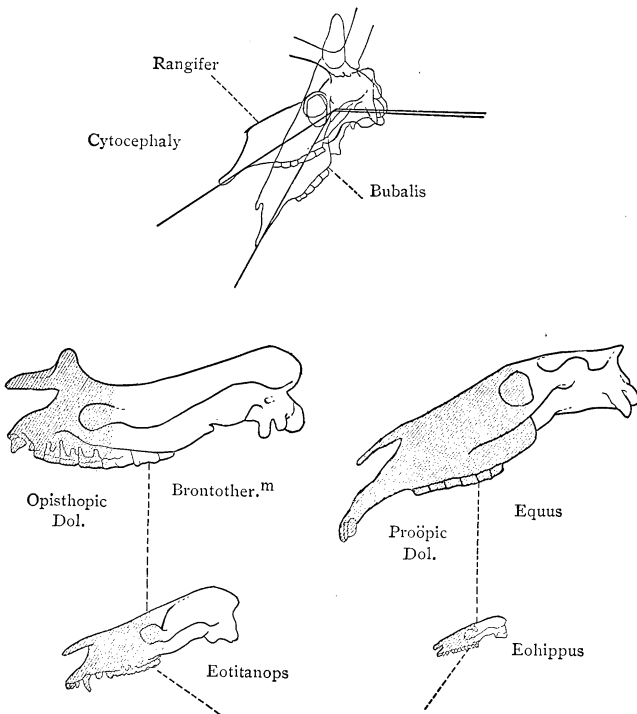


FIG. 4. CONTINUOUS ORIGIN OF ALLOMETRIC "UNIT CHARACTERS" IN THE SKULL OF VARIOUS UNGULATES.

C Cytocephaly,

D Dolichocephaly,

Bubalis

Opisthopic  
(Titanotheres)

Rangifer.

Proöpic.  
(Equines).

In the ancestral *Eotitanops* and *Eohippus* the facio-cranial index is very similar. In the descendants of these animals, as indicated by the dotted lines, the facio-cranial indices are widely divergent; in the Titanotheres (*Brontotherium*) the cranium is elongated; in the horses (*Equus*) the face is elongated.

cephaly of the Alpine type, recalling the broad-headed Asiatic type of skull. Thus (Ripley, p. 56) "pure physical types come in contact and this means ultimately the extinction of extremes." Applying these principles to the present case, it implies the ultimate blending of the long and the narrow heads and the substitution of one of medium breadth.

Elliot Smith also (letter, August 12, 1911) implies a gradual modification or blending of head form through prolonged intermixture. He observes:

Egypt does not give a clear answer to your queries because her exceedingly dolichocephalic brown race [related to the Mediterranean race of southern Europe] underwent a double admixture (circa 3,000 B.C.) with moderately brachycephalic "Armenoids" from Asia and dolichocephalic Negroes from Africa. The Mediterranean Egyptians are on the whole a little broader-headed than they were 6,000 years ago, and this *may* be due in part to a slow development toward mesaticephaly; but it is mainly the result of an admixture with alien brachycephalics and mesaticephalics. There is an unquestionable tendency toward the elimination of the extremes of narrowheadedness and broadheadedness.

Hrdlička (letter, December 5, 1911) observes:

As to the effect of the mixture of brachycephalic and dolichocephalic individuals or peoples, I am led to believe that there is in the results of such mixtures a large percentage of more or less intimate "blend" of the two forms, for such a condition is indicated by the curves of distribution of the cephalic index among such national conglomerates as the French, Germans, different tribes of the American Indians, etc. These curves, if sufficiently large numbers of individuals have been examined, all approach more or less the ideal camel-back curve. If no "blend" existed, we should be bound to get the double or dromedary-back curve. Of course the effects of mixture and the effects of environment are with our present means often impossible of separation, they often obscure each other. Yet the indications are that there is generally a considerable amount of more or less mixture of the many elementary constituents of the hereditary characters [known collectively as] dolichocephaly and brachycephaly. With this there coexists doubtless some tendency toward a differentiation into the two opposite forms of the head.

Thus in human head form we have proofs of continuous

allometric change strictly comparable to that which occurs in the crania of lower mammals, especially as observed in the horses and titanotheres; the extremes are produced in so-called pure human races under geographic isolation; when these pure races are brought together there arises disharmonism or alternating heredity or both. Neither the dolichocephalic nor brachycephalic type is as yet known to be dominant; opinion is divided as to whether in the first cross the heredity is pure or whether there may be a tendency to produce an intermediate form; opinion is nearly unanimous that prolonged interbreeding produces blends.<sup>36</sup>

#### 4. *Skull of Titanotheres.*

The continuity of allometric evolution in the skull of the titanotheres (Fig. 4) has been the subject of prolonged investigation by the writer, assisted by Dr. W. K. Gregory, involving thousands of measurements, many of which belong in strictly successive phyletic series. Allometry (*i. e.*, the measurement of allometrons) here applies to the skull as a whole. We secure the cephalic index by dividing the breadth across the cheek arches by the total basilar length of the skull. There are also other indices, such as the facio-cranial, in which we measure continuous trends of allometric change; brachycephaly and dolichocephaly arise independently in four different phyla or lines of descent. The adaptive significance is sometimes apparent, sometimes obscure. As shown in Fig. 1 the titanotheres, like man, exhibit facial abbreviation and cranial elongation (postopic dolichocephaly) in contrast with the facial elongation (proopic dolichocephaly) of the horses. These phenomena are similar to those of cytocephaly, or the bending down of the face upon the base of the cranium as observed in the reindeer

<sup>36</sup> T. H. Morgan observes that a blend may occur in the first generation, F<sub>1</sub>, even where perfect segregation occurs in F<sub>2</sub>. The results of crossing the equine skull as described below indicate a tendency to blend in the first cross.

(*Rangifer*) and the hartebeest (*Bubalis*). Cytocephaly is an ontogenetic and phylogenetic new character, arising or developing continuously.

As in the case of the human skull, the causes of these profound changes in head form are entirely unknown; the mechanically adaptive significance is sometimes apparent, sometimes obscure. The evidence is strengthened by the examination of the titanotheres that human selection has little or no influence on human cranial form. The great point to emphasize is that *this allometric evolution in the skull and all parts of the skeleton is the prevailing phenomenon of change in the skeleton of mammals*. It is constantly in progress and is universally, so far as we can observe, a continuous process. As displayed in the four phyla of titanotheres (Fig. 3), the elongation or broadening of the foot bones proceed independently and are *divergent*, while in the same mammals the rectigradations exhibited in the rise of similar cusplets on the teeth and similar horn rudiments on the face are *parallel*; in the former case no ancestral predisposition seems to be operating, in the latter case ancestral predisposition certainly seems to operate; this is why the internal laws controlling the origin of new allometrons and of new rectigradations and allometrons are regarded as essentially dissimilar.

Paleontological analysis of these rectigradations and allometrons even unaided by experimental heredity reveals the essential feature of the "unit character" principle, namely, *that what we are observing is an incredibly large number of unit elements each of which enjoys a certain independence of evolution at the same time that each unit is adaptively correlated with all the others*. For example, in the upper and lower grinding teeth of horses alone there are 504 cusp units, each of which has an independent origin and development; at the same time each cusp is more or less distinctly correlated in form with the all-pervading dolichocephaly or brachycephaly of the skull; in fact, from certain single cusps of the teeth we

can often determine whether the animal is brachycephalic or dolichocephalic.

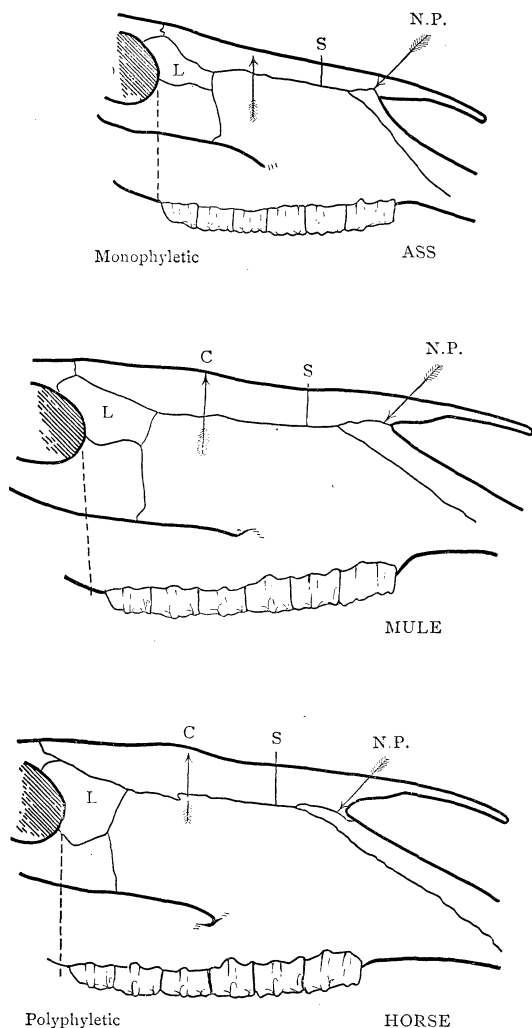


FIG. 5. CROSS-BREEDING AND IMPERFECT BLENDING OF ALLOMETRIC "UNIT CHARACTERS" OF THE FACIAL BONES IN ASS (MALE), HORSE (FEMALE) AND MULE.

Bones of the side of the face, Ass.

Bones of the side of the face, Mule.

Bones of the-side of the face, Horse.

The horse is certainly polyphyletic, the ass is probably monophyletic. *C*. The arrow points to *C*, a distinct bump in the horse and mule, not observed in the ass. *S* = point at which the section of the nasals is taken. *L* = lachrymal. *N.P.* = naso-premaxillary suture.

The question arises as a result of the somewhat conflicting evidence as to the crossing of brachycephals and dolichocephals in man, what happens when we cross two phyla of lower mammals which have been diverging along separate allometric lines and in the meantime have acquired a greater or less number of new characters which when sufficiently developed attain specific rank.

The answer is given very distinctly in the cross between the dolichocephalic horse (*E. caballus*) and the mesocephalic ass (*E. asinus*). Here we learn again that profound differences have been established through continuity and that we are enabled to split up these differences into distinct or partially blending units through cross breeding.

### 5. *Blended or Alternating Heredity in Horses.*<sup>37</sup>

So high an authority as J. Cossar Ewart (1903) has sustained the prevailing view that in the mule there is generally an imperfect blending of the characters of the immediate parents; the same author, however, notes that mules occasionally serve as examples of unit or exclusive inheritance.<sup>38</sup> He cites two cases: (1) a mule out of a well-bred, flea-bitten New Forest pony closely resembles her sire, the ass; (2) a "calico" mule, on the other hand, is surprisingly like his dam, an Indian "painted" pony. This painted mule demonstrates that the ass is not always more prepotent than the horse. From this author's very extensive breeding experiments the following conclusions are reached: the less fixed or racially valuable characters

<sup>37</sup> The writer is indebted to Mr. S. H. Chubb, Mrs. Johanna Kroeber Mosenthal and to Dr. W. K. Gregory for many of the observations and all of the measurements on which this comparison is based. The materials studied are three skulls of the ass (♂ *E. asinus*), ten of the horse (♀ *E. caballus*), and four of the mule, all adult with teeth in approximately the same stage of wear.

<sup>38</sup> The most recent (1912) opinion of Ewart is much more positive as to the operation of Mendel's law in pure breeding strains of horses. See "Eugenics and the Breeding of Light Horses," *The Field*, February 10, 1912, pp. 288, 289.

of zebras either blend with or are dominated by the corresponding characters in their horse and ass mates. Thus, as influencing dominance or prepotency, the value which a character has attained in the past struggle for existence seems to count for something. In zebras and in horses certain physical and mental traits are more highly heritable than others. Among the characteristics which are often handed down unblended in zebra-horse hybrids and to a less extent in zebra-ass hybrids are the size of the ears, the form of the hoofs, the massiveness of the jaws; while among psychic characters are transmitted the extreme caution, the wonderful alertness and quickness.

The new results brought forward in this Harvey lecture from the comparison of the skull and teeth of the horse, ass and mule on the whole strengthen the theory of unit inheritance both in rectigradations and in allometrons. The measure of unit character inheritance as contrasted with blended inheritance is very precisely brought out in the detailed study of the twenty-two characters which are examined below. Before discussing these characters in detail it is interesting to point out that the ancestors of the horse and the ass have probably been separated for at least 500,000 years. In the meantime the horse has become extremely dolichocephalic, the ass has remained comparatively mesocephalic; the horse has a relatively long, the ass a relatively short face; the horse has highly complex, the ass has somewhat simpler grinding teeth; the horse exhibits advanced adaptation to grazing habits and has become habituated to a forest and plains life in comparatively fertile countries, while the wild ass is by preference a browsing animal, finding its food in excessively arid countries where there is a marked dearth of water and water courses. The physical and psychical divergences in these two animals have developed over an enormously long period of time. Every single tooth and bone of the horse and ass show differences both in rectigradation and in allometric evolution.

One feature which tends to make the results of the cross less clear and distinctive than they are is that while the ass is monophyletic (being descended with

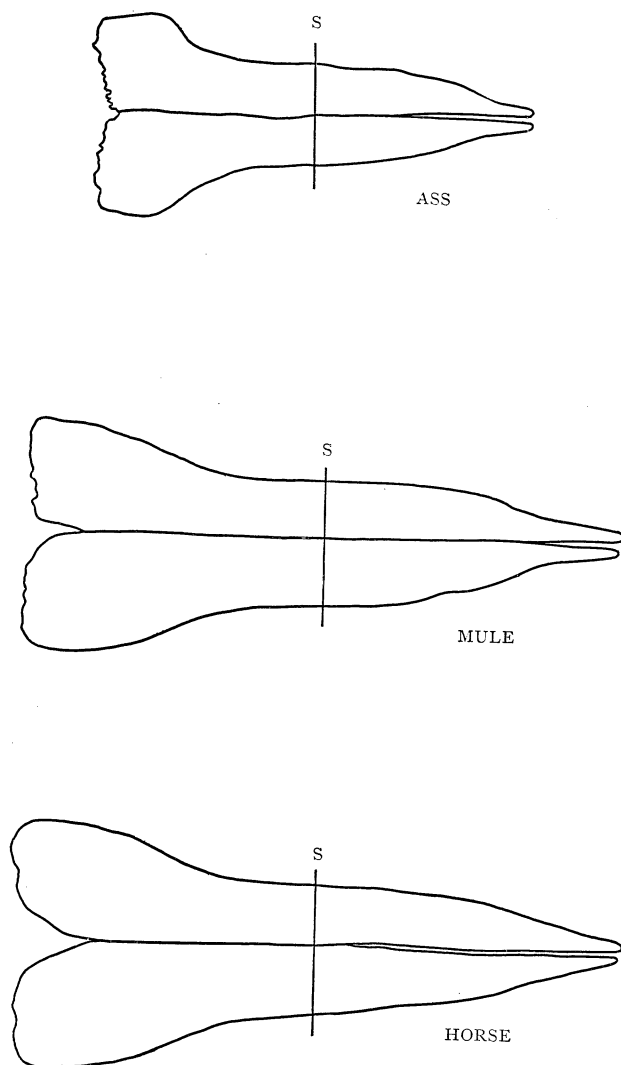


FIG. 6. CROSS-BREEDING AND IMPERFECT BLENDING OF SUB-ALLOMETRIC "UNIT CHARACTERS" OF THE NASAL BONES IN ASS (MALE) AND HORSE (FEMALE).

Top view of nasals and naso-frontal suture, Ass.

Top view of nasals and naso-frontal suture, Mule.

Top view of nasals and naso-frontal suture, Horse.

S = point of section shown in Figs. 3 and 5.

modification from the wild *E. asinus* of northern Africa), the domestic horse is not a pure strain and is certainly polyphyletic, having in its blood that of several races, such as the Arab and the Forest or Norse horse, animals which have specific distinctness although they still interbreed.<sup>39</sup> To this mixed strain or polyphyletic heredity of the horse, are probably attributable many of the allometric variations in the bones of the skull and in the enamel pattern of the teeth of the mule in some of which we observe a nearer approach to the ass type than in others. If we could cross the ass with a pure horse race like the Steppe or Prjevalsky horse we should probably obtain more precise results. Another disturbing feature in the comparisons and indices given below is that we do not know the exact structure of the skull of either of the parents from which the mule skulls examined were derived.

Despite these sources of fluctuation and of error, the general results obtained are fairly positive and definite.

The first point of interest in the segregation of unit characters in the mule is that connected with the *three germinal layers*, namely, the epiblast, mesoblast and hypoblast. All the characters of epiblastic origin appear to be derived from the sire, namely, the epidermal derivatives, the distribution of the hair, especially in the mane and tail, the hoofs, etc., are those of the ass, although the color pattern, as in the "calico" mules described by Ewart, may be derived from the mare. The nervous system and psychic tendencies, all of epiblastic origin are also derived from the ass, including minor psychic characteristics, such as aversion to water. Still more striking, perhaps, is the fact that the enamel pattern of the grinding teeth, again of epiblastic origin, is mainly that of the ass, although, as shown below, there are some intermediate and some distinctive horse-like characters in the

<sup>39</sup> There are many absolute characters which separate the Arab from the Norse horse, among them the invariable presence of one less vertebra in the lumbar region of the back.

teeth of the mule; this may be partly connected with the mesoblastic derivation of the dentine of the teeth.

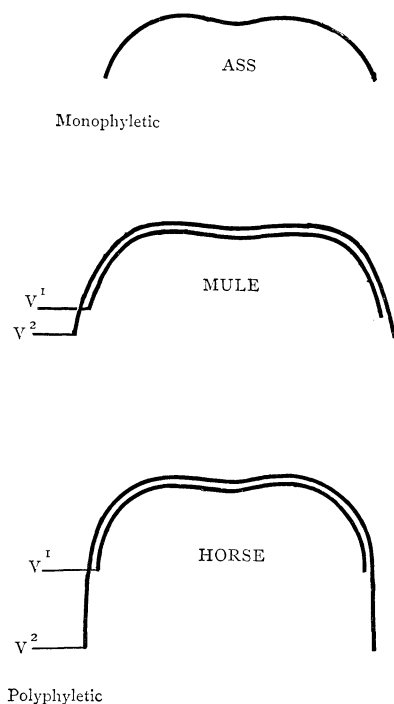


FIG. 7. CROSS-BREEDING AND IMPERFECT SEPARATION OF ALLOMETRIC "SUB-UNIT CHARACTERS" OF THE NASAL BONES IN ASS (MALE), HORSE (FEMALE) AND MULE.

Mid-section of nasal bones, Ass.  
 Mid-section of nasal bones, Mule.  
 Mid-section of nasal bones, Horse.

$V^1, V^2$  = variations in the depth of the nasals in the mule.  $V^1, V^2$  = variations in the depth of the nasals in the horse.

Mesoblastic derivatives, on the other hand, are divided between the sire and dam, the skeleton and limbs of the mule being mainly proportioned as in the ass, while the skull of the mule, as we shall see, is almost purely that of the horse.

*Blended and Pure Inheritance in the Bones of the Face*  
*Blending.*—A comparison of the bones of the side of

the facial or preorbital region shows intermediate or partly blended form and proportions both of the *nasals*, *premaxillaries*, *frontals*, and *lachrymals*, in which, however, the mule approaches *E. caballus* rather than *E. asinus*. Attention may be called to some of the details of the comparison: (1) *Suture between the nasals and premaxillaries*: in *E. asinus* short and elevated, in the mule intermediate but more like the horse; in the horse elongated and depressed (see Fig. 5). (2) *Naso-frontal suture on the top of the skull*: in the ass straight or transverse; in the mule incurved, more like the horse than the ass; in the horse arched or incurved (see Fig. 6). (3) *Depth and convexity of the nasals*: in the ass shallow and flattened; in the mule deeper, more like the horse; in the horse highly arched. (4) *Bump or convexity on posterior third nasals*: in the ass very slight; in the mule moderate, more like the horse than the ass; in the horse strong (see Fig. 7).

The same tendency in the mule to exhibit a slight departure from the horse toward the ass type is shown in the outlines of the bones of the face (Figs. 3, 4, 5). Comparing step by step the premaxillaries, maxillaries, nasals, and lachrymals, while the proportions and the sutural outlines are mainly those of the horse, there is a more or less distinct blending, or intermediate character in the direction of the ass; see especially the naso-premaxillary suture, the degree to which the nasals extend downward on the sides of the face to join the maxillaries, and the degree to which the nasals extend on the sides of the face to join the maxillaries. In this naso-maxillary junction certain horses approach the ass type. The characteristic bump on top of the nasals of the horse is transmitted to the mule, and the highly characteristic transverse suture between the frontals and the nasals, as seen from the top (Fig. 4), is rather that of the horse than of the mule.

*Non-blending*.—More definite results are shown in the heredity of the indices or ratios between the various por-

tions of the skull and of the teeth; these indices are extremely constant allometric specific characters, they are independent of size. For example, the indices of a diminutive pony and of a giant percheron would be the same. Similarly the indices of a diminutive donkey and of a very large ass would be the same.

The index is the best and most exact form of expressing mathematically the profound differences between the skull of the horse and that of the ass. Indices have the value of specific characters; they are of especial significance in the present discussion in comparison with those in the face, cranium and palate of man and of the titanotheres above considered.

Chief among the allometric differences are the following: (1) In its proportions the ass has a relatively shorter space between its grinding and its cutting teeth, the bit-opening; this is correlated with the fact (2) that the ass has a relatively broader and shorter skull than the horse; also with (3) the fact that the ass has a relatively longer cranium (postorbital space) and shorter face (preorbital space) than the horse; (5) the ass also has relatively broader grinding teeth correlated with the broader skull; (6) correlated also with its less elongate skull the ass has a relatively rounder orbit than the horse, *i. e.*, the vertical and horizontal diameters are more nearly equal. (7) A very distinctive feature is the angle which the occiput makes with the skull; this is one of the marked specific features of the ass.

#### NON-BLENDING OR PURE INHERITANCE INDICES IN THE SKULL

1. Cephalic Index:	$\frac{\text{Width of skull} \times 100}{\text{Basilar length}}$	Ass	46.9-49.9
		Mule	40.8-43.6
		Horse	40.4-44.1
2. Diastema Index:	$\frac{\text{Diastema} \times 100}{\text{Basilar length of skull}}$	Ass	15.6-17.6
		Mule	18.6-21.9
		Horse	18.2-23.0
3. Cranio-facial Index:	$\frac{\text{Length of cranium} \times 100}{\text{Length of face}}$	Ass	56.3-61.0
		Mule	48.9-51.8
		Horse	45.3-49.9

4. Orbital Index:	Vertical diameter of orbit $\times 100$	Ass	96.0-104.2
	<hr/> Horizontal diameter	Mule	78.7- 99.1
		Horse	84.2- 93.5
5. Molar Index:	Transverse diameter of M <sup>2</sup> $\times 100$	Ass	15.2-16.0
	<hr/> Total length of entire molar series	Mule	14.2-14.9
		Horse	13.9-15.7
6. Occiput-vertex angle Index:	Angle between vertex of skull and line connecting most posterior points of occipital crest with condyles,	Ass	52.5-60.0
		Mule	61.0-66.5
	<i>i. e.</i> , nearly all horse skulls will stand when set up on end, some mule skulls (one out of four), no ass skulls	Horse	64.0-76.5
7. Vomer Index:	Distance from palate to posterior end of vomer $\times 100$	Ass	93.8-111.7
		Mule	95.5-110.3
	<hr/> Distance from vomer to foramen magnum	Horse	72.8- 86.5

The above indices prove that the mule has not a primitive skull like that of the ass on a larger scale, but has essentially the skull of the horse, namely:

1. A long, narrow skull, as a whole.
2. A long diastema, or space for the bit.
3. A short cranium and a long face.
4. A long, oval orbit.
5. A relatively elongate and narrow set of grinding teeth.
6. A vertically placed occiput.

The one character in which the mule resembles the ass is the elongation of the vomer behind the bony palate. It should, however, be distinctly stated that while the indices given above are those which probably prevail in mules, there are overlaps in the (4) orbital index and (6) occiput-vertex angle. Thus in one mule the orbital index agrees with that of one of the asses.

*Enamel Pattern of Grinding Teeth.*—In the marvelously complex pattern of the grinding teeth the “unit character” transmission is quite sharply defined in the majority of characters, while intermediate or slightly blended in the minority. In general in the grinding teeth of the ass the main enamel folds are less complicated

than in the horse and there are fewer secondary or subsidiary folds; the ass especially lacks the "pli caballin" (fold 5) which is usually a very pronounced specific character of the horse. The mule shows a very slight indication of this fold and thus resembles the ass. The

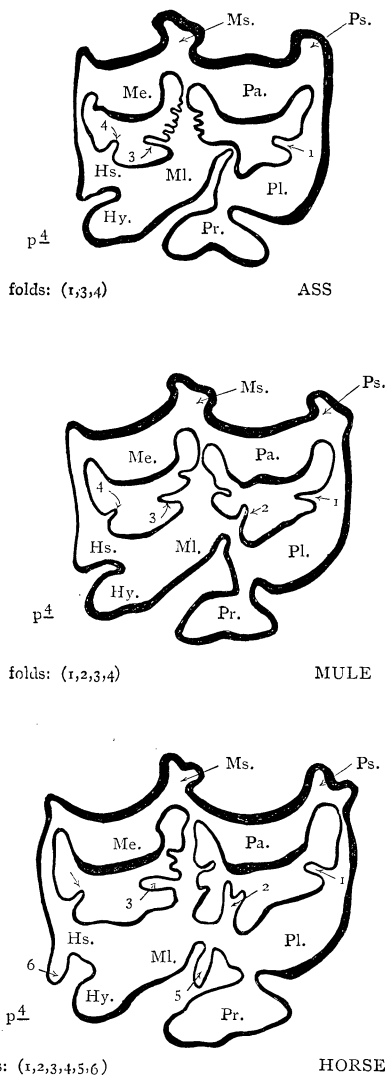


FIG. 8. CROSS-BREEDING AND SEPARATION OF RECTIGRADATIONS, DISTINCT "UNIT CHARACTERS" IN THE ENAMEL FOLDINGS AND PATTERN OF THE GRINDING TEETH OF THE ASS, MULE AND HORSE. Section through the crown of the third superior grinder ( $p^4$  or 4th premolar) ass (male), horse (female) and mule.

subsidiary folds in the grinders of the mule are simpler than those in either the horse or the ass. The grinder of the mule would be pronounced by any systematist not knowing its mixed parentage to belong to the ass rather than to the horse, especially in the absence of the “pli caballin” (fold 5), in the form of the hypostyle (*hs*, fold 6), in the smaller size of the protocone (*pr*), the large size of which is very distinctive of the horse. A very detailed study and comparison of the grinding teeth in the horse, ass and mule made by an independent observer, Dr. W. K. Gregory, gives the following result:

Secondary folds :	protocone,	<i>pr.</i>	
	paracone,	<i>pa.</i>	
	metacone,	<i>mc.</i>	
	hypocone,	<i>hy.</i>	
	protoconule,	<i>pl.</i>	
	metaconule,	<i>ml.</i>	
Secondary elements :	parastyle,	<i>ps.</i>	
	mesostyle,	<i>ms.</i>	
	hypostyle,	<i>hs.</i>	
Primary elements :	fold 1	..... Horse	..... Mule
	fold 2	..... Horse	..... Mule
	fold 3	..... Horse	..... Mule
	fold 4	..... Horse	..... Mule
	fold 5	..... Horse.	

#### UNIT CHARACTERS IN GRINDING TOOTH OF THE MULE

Distinctly ass-like:	5 characters	} 11 peculiar to ass.
Less distinctly ass-like:	6 characters	
Common to horse and ass:	5 characters	5 common to horse and ass.
Distinctly horse-like:	2 characters	} 6 peculiar to horse.
Less distinctly horse-like:	4 characters	

It would be especially desirable to compare the same enamel characters in the hinny, which is a cross between the male horse and the female ass, in which it is well known that the *E. caballus* and *E. asinus* characters are differently distributed.

*Summary.*—Out of the 28 characters examined in the skull and teeth of the mule, 18 are distinctly derived either from one parent or the other with very slight, if any, tendency to blend, 10 characters show a distinct tendency to blend.

This evidence, in the opinion of T. H. Morgan, is in entire accord with the modern views of hybridizing; parallels for each instance can be given; without the evidence of the  $F_2$  generation no conclusions adverse to Mendelism are possible. Even the differences in reciprocal crosses, *i. e.*, horse ♂, ass ♀, can be understood if sex-limited inheritance prevails in some characters.

To confirm the results suggested by this  $F_1$  generation of the horse and ass, it would be necessary to interbreed races of mammals to  $F_2$  or  $F_3$  to ascertain whether these characters of the skull and teeth really mendelize. It is doubtful whether such specific types of mammals can be found, and whether sufficient stability of character exists in artificially produced races.

Sufficient evidence has been adduced, however, to show that a very large number of characters which are to the best of our knowledge of continuous origin, present all the appearance of "unit characters" in the first generation of hybrids.

### III. CONCLUSION

Is it not demonstrated by this comparison of results obtained in such widely different families as the Bovidae, Hominidae, Titanotheriidae and Equidae that *discontinuity in heredity affords no evidence whatever of discontinuity of origin?*

As to origin, it is demonstrated in paleontology that certain new characters arise by excessively fine gradations which appear to be continuous. If discontinuities or steps exist they are so minute in these characters as to be indistinguishable from those fluctuations around a mean which seem to accompany every stage in the evolution and ontogeny of unit characters.

### IV. THEORETICAL CONSIDERATIONS

After having attempted to confine our discourse to facts it is a pleasure to relax into the more genial atmosphere of opinion and hypothesis.

The principle of pre-determination, which results in the appearance of rectigradations, involves us in radical opposition to the opinions of the Bateson-DeVries-Johannsen school. There is an unknown law operating in the genesis of many new characters and entirely distinct from any form of indirect law which would spring out of the selection of the lawful from the lawless. This great wedge between the "law" and the "chance" conception, which since the time of Aristotle has divided biologists into two schools of opinion, is driven home by modern paleontology.

Paleontology, in the origin of certain new characters at least, compels us to support the truly marvelous philosophic opinion of Aristotle, namely:

*Nature produces those things which, being continuously moved by a certain principle contained in themselves arrive at a certain end.*

While recent biology has tended to sharply distinguish bodily from germinal processes and to place chief emphasis upon evolution appearing to originate in the germ cells, we must not forget that for a hundred million years or more, or from the beginning of life, the germ plasm has had both its immediate somatic and its more remote environmental influences. Because the grosser form of Lamarckian interpretation of transmission of acquired characters has apparently been disproved, we must not exclude the possibility of the discovery of finer, more subtle relations between the germ plasm and the soma, as well as the external environment. There are several phenomena, which have been observed only in paleontology, that afford evidence for the existence of such a *nexus*; because it appears that certain germinal predispositions to the formation of new characters, connected, as Darwin conjectured, in some way with community of descent, are only evoked under certain somatic and environmental conditions, without which they appear to lie in a latent, potential or unexpressed form.

All that we may be able to observe are the *modes* of

operation in the genesis of new characters and in the adaptive trends of allometric evolution without gaining any intimate knowledge of what the *causes* are. This thought may be made clear through the following analogy. Naturalists observed and measured the rise and fall of the tides long before Newton discovered the law of gravitation; we biologists are simply observing and measuring the rise and fall of the greater currents of life. It is possible that a second Darwin may discover a law underlying these phenomena bearing the same relation to biology that the law of gravity has to physics, or it is possible that such law may remain forever undiscovered. Another analogy may make our meaning still clearer. Ontogenesis is inconceivable, for example, the transformation of an infinitesimal speck of fertilized matter into a gigantic whale or dinosaur; we may watch every step in the process of embryogeny and ontogeny without becoming any wiser; in a similar sense phylogenesis may be inconceivable or beyond the power of human discovery. Not that we accept Driesch's idea of an entelechy or Bergson's metaphysical projection of the organic world as an individual, because we must believe that the entire secret of evolution and adaptation is wrapped up in the interactions of the four relations that we know of, namely, the germinal, the bodily, the environmental, with selection operating incessantly as the arbiter of fitness in the results produced. In the meantime<sup>40</sup> we paleontologists have made what appears to be a substantial advance in finding ever more convincing evidence of the operation of law rather than of chance in the origin and development of new characters, something which Darwin had clearly in mind.<sup>41</sup>

<sup>40</sup> Osborn, H. F., "The Hereditary Mechanism and the Search for the Unknown Factors of Evolution," Biol. Lect. Marine Biol. Lab., 1894, AMER. NATURALIST, Vol. XXXIX, No. 341, May, 1895, pp. 418-439.

<sup>41</sup> Darwin, Chas.: "I have spoken of variations sometimes as if they were due to chance. This is a wholly incorrect expression; it merely serves to acknowledge plainly our ignorance of the *cause* of each particular variation."